Recent Advances in Studies on Mesozoic and Paleogene Mammals in China

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Like in other fields of paleontology, research in paleomammalogy mainly falls into two aspects. One is related to the biological nature of fossil mammals, such as their systematics, origin, evolution, phylogenetic relationships, transformation of key features and paleobiogeography, and the other is related to the geological context, involving biostratigraphy, biochronology, faunal turnover and its relations to the global and regional environmental changes. In the last decade, a number of well-preserved mammalian specimens were collected from different localities around the country. Such discoveries have provided significant information for understanding the early evolution of mammals and reconstructing the phylogeny of early mammals.

Studies of Chinese Mesozoic mammals achieved remarkable progress in the past several years. Nineteen species of 17 genera of Chinese Mesozoic mammals have been named since 2005. Among these species, some preserved the key features that are informative for understanding the mammalian history.

Among these key features significant for mammalian evolution, one is critical to the improvement of hearing capability. The mammalian middle ear, which is considered as one of the most important innovations during mammalian evolution, has three ear ossicles: malleus, incus and stapes. Of these three ossicles, only stapes is present in fossil and living reptiles. The malleus and incus, derived respectively from the articular of the lower jaw and the quadrate of the cranium following the process of reduction and detachment from the reptilian mandible, are new elements of the bony chain in the mammalian middle ear. The appearance of mammalian middle ear allows mammals to hear the sound of higher frequencies than reptiles do. Generally speaking, a widely accepted hypothesis is that mammals originated from a certain extinct reptilian group. The formation and development of the definitive mammalian middle ear (DMME) has thus become one of the key issues in the study of mammalian evolution and has drawn the attention from many researchers for many years.

Developmental biological studies have proven the function of the Meckel's cartilage and its relationship to the ear ossicles during the development of mammalian middle ear, but no fossil evidence was reported until 2001. The discovery of the ossified Meckel's cartilage (OMC) in *Repenomamus* first provided fossil evidence supporting the relationship between the ear ossicles and the Meckel's Cartilage, which is coincident with the result of embryo developmental biology (Wang *et al.*, 2001). Since then, the OMCs have been recognized in different taxa, such as *Gobiconodon* (Li *et al*., 2003), *Zhangheotherium* (Meng *et al.*, 2003), *Yanoconodon* (Luo, Chen *et al*., 2007), and *Maotherium* (Ji *et al.*, 2009). However, middle ear ossicles were never found in the fossil record of primitive mammals until quite recently, when they were at last reported to be

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connected to the mandible via an OMC in the triconodont *Yanoconodon allins* from the Yixian Formation in Fengning, Hebei Province (Luo, Chen *et al.*, 2007). The connected ear ossicles and jaw structure are similar to the embryonic pattern in modern monotremes (egg-laying mammals) and placental mammals. All these findings clearly suggest the presence of a stage during the DMME development, at which the reduced ear bones are in connection to the mandible via the Meckel's cartilage, no matter ossified or unossified.

Another important feature is related to the feeding function of mammals. All living mammals except monotremes have a tribosphenic pattern in their upper and lower molars. The tribosphenic upper molar has a lingual cusp (protocone) that occludes within the basined talonid of the lower molar. Such kind of molars is capable of shearing and grinding during occlusion and makes possible the function of chewing, which is exclusively a mammalian feature. The transformation from a non-tribosphenic pattern to a tribosphenic one has been documented in some fossil record. However, a different type of molars was recognized as pseudotribosphenic pattern based on a left lower jaw of *Shuotherium dongi* from the Upper Jurassic of Sichuan (Chow and Rich, 1982). In contrast to the tribosphenic pattern, in which the basined talonid is posterior to the trigonid that is formed of three main cusps (paraconid, metaconid and protoconid) in the lower molar, the pseudotribosphenic lower molar possesses a pseudotalonid anterior to the trigonid. Based on the structure of the lower molars of *Shuotherium*, a pseudoprotocone is hypothesized for its corresponding upper molars. This was further supported by an isolated upper molar of *S. shilongi* found from the same locality (Wang *et al.*, 1998), but the discovery of *Pseudotribos robustus* from Jurassic of Inner Mongolia with its upper and lower molars in occlusion rigorously corroborated the original hypothesis, demonstrating that a pseudoprotocone is present on the upper molars and occludes with the pseudotalonid on the lower molar (Luo, Ji *et al.*, 2007). These findings provide strong evidence to support that the tribosphenic condition, a key innovation in the history of mammals, could well have arisen more than once, despite its complexity.

Issues more interesting to the public than the transformation of some key mammalian features include those related to the mammalian behavior, locomotion, and diets. For many years, Mesozoic mammals were thought to have been moving on the ground or dwelling in the tree (Fig. 1) (Hu and Wang, 2002; Ji *et al.*, 2002; Luo *et al.*, 2003), but the recent discoveries suggest more possibilities.

Recently, two Mesozoic mammals were found from the Jurassic of Ningcheng, Chifeng, Inner Mongolia. One of them, *Castorocauda lutrasimilis*, is a representative of docodonts, a fairly primitive mammalian group. Its postcranial skeletal and dental features indicate swimming and burrowing adaptation and aquatic feeding. The animal was thus inferred to as semiaquatic (Ji *et al*., 2006). The other, characterized by a highly specialized insectivorous dentition, represents a completely new form of primitive mammals, and was named *Volaticotherium antiques* in its own order Volaticotheria. A sizable patagium (flying membrane), covered with dense hair and supported by an elongated tail and limbs, suggests that the animal has the ability of gliding between trees. Because the gliding mammal was previously unknown from the Mesozoic era, this discovery extends the earliest record of gliding flight for mammals by at least 70 million years in geological history (Meng *et al*., 2006). The discoveries of these animals demonstrate that some Mesozoic mammals developed diverse locomotory strategies and lifestyles and were ecomorphologically different from the majority of generalized small terrestrial Mesozoic mammals.

Fig. 1 Lifestyle reconstruction of the multituberculate *Sinobaatar lingyuanensis*. (Drawn by Mr. XU Yong)

It was long believed that Mesozoic mammals were all small-sized like a living tree shrew and lived in the shadow of dinosaurs. However, such consideration has been changed since the discovery of *Repenomamus giganticus* from the Lower Cretaceous Yixian Formation in western Liaoning. This animal, over one meter long, weighs up to 12–14 kilograms and is considered the largest of the Mesozoic era. Surprisingly, its sharp anterior teeth and robust lower jaws have clear similarities to those of predator mammals. Even more surprisingly, a specimen of smaller *R. robustus* from the same area provides direct evidence for the carnivorous nature of *Repenomamus*. In the stomach area of the specimen, some digested bone fragments of a juvenile *Psittacosaurus*, a ceratopsian dinosaur, were preserved. Careful examination suggests that *Repenomamus* not only fed on small dinosaurs, but also swallowed large pieces without chewing (Hu *et al.*, 2005).

In the study of Paleogene mammals, research on the

Lifestyle reconstruction of *Repenomamus*. (Drawn by Mr. XU Xiaoping)

origin and evolution of primates is always a hot topic not only for scientists but also for the public. Chinese scientists have made significant contributions in this field.

The best Paleogene primate that has ever been discovered in Asia is *Teilhardina asiatica* from the earliest Eocene of Hunan Province. It is widely accepted to represent the earliest and most primitive primate with modern aspects. Despite having very primitive insectivore-like teeth, this species already developed convergent orbits and a quite enlarged brain case, derived features shared by all primates. Morphometric study and multivariable statistic analysis indicate that this species is probably a diurnal (active in daytime) animal. By tracing the activity pattern across a phylogenetic tree, we postulated that the last common ancestor of primates was a small-bodied, diurnal and vision-guided insect predator. This scenario changed the traditional idea of a nocturnal origin of primate (Ni *et al.*, 2004).

The place of origin and early dispersal routes of primates are the main topics in research about the origin and evolution of primates. The recent discoveries of Paleogene primates have provided compelling evidence for the Asian origin hypothesis. The ancestor of primates, which is probably very close to *Teilhardina asiatica*, very likely originated from Asia, then dispersed to Europe and North America (Ni *et al.*, 2005). New discoveries of the Early and Middle Eocene primates from Inner Mongolia indicate that dispersal of primates from Asia to North America may have occurred many times (Ni *et al.*, 2010).

A significant progress in Paleogene mammal research in recent years also helps understand the faunal turnover and radiation through geological time. By analyzing the mammalian faunal composition and changes, three stages are recognized in the Paleogene mammalian radiation: (1) the Paleocene flourishing of archaic groups, (2) the Eocene rising and development of modern major groups and (3) the Oligocene faunal reorganization. During the Paleocene, the mammalian radiation was dominated by the archaic groups and the faunas showed apparent endemism. The radiation was characterized by faunal turnovers due to the flourishing of different families in archaic groups. During this period, ancestral forms of modern glires emerged and the first Rodentiaformes appeared in the late Late Paleocene. Such faunal changes corresponded to the successive rise of temperature after the transition from the Mesozoic to the Cenozoic. The Paleocene-Eocene Thermal Maximum resulted in a significant decrease of the archaic groups and the faunal composition became more similar to that of modern ones. At the beginning of the Eocene, Artiodactyla and Euprimates appeared and Rodentia and Perissodactyla began to differentiate. During the Eocene, Perissodactyla became the dominant group in the faunas. The faunal turnovers were characterized by the alteration of dominant families due to the appearance, differentiation and flourishing of families in modern orders. The severe cooling events at the Eocene–Oligocene transition resulted in the development of open grassland, and further contributed to the great mammalian faunal turnover. The perissodactyl-dominant Eocene faunas were replaced by the rodent/lagomorph-dominant Oligocene faunas. The appearance and radiation of mammal groups with high-crowned cheekteeth characterized the mammalian evolution in the Oligocene (Wang *et al.*, 2007).

The Cenozoic is called the "Era of Mammalia." Fossil mammals are adopted as the basis of the Cenozoic biostratigraphic correlation. Land Mammal Ages serve as the biostratigraphical and biochronological units in the related Cenozoic research without exception in the Paleogene. A number of Asian Land Mammal Ages (ALMAs) were proposed on the basis of Chinese Paleogene mammal faunas, and thus the research on Chinese Paleogene mammals has played an important role in establishing the framework of ALMAs. Although the ALMAs have been widely used for many years, they are not well constrained. Recent paleomagnetic work in both southern and northern China provides new information for correlating some ALMAs to the global geological time scale. This not only helps to define some key geological boundaries and adjusts the age determination of the related ALMAs, especially of the early Paleocene through the middle Eocene, but also makes it possible to discuss biological events in the global environmental context (Wang, Meng *et al.*, 2010 (in press); Wang, Tong *et al.*, 2010 (in press)).

References

Chow M C, Rich T H V, 1982. *Shuotherium dongi*, n. gen. and sp., a therian with pseudo-tribosphenic molars from the Jurassic of Sichuan, *China. Aust Mammal*, 5: 127–142.

Hu Y M, Meng J, Wang Y Q *et al.*, 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature*, 433: 149–152.

Hu Y M, Wang Y Q, 2002. *Sinobaatar* gen. nov.: First multituberculate from the Jehol Biota of Liaoning, Northeast China. *Chinese Sci Bull*, 47(11): 933–938.

Ji Q, Luo Z X, Yuan C-X *et al.*, 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science*, 311(5764): 1123–1127.

Ji Q, Luo Z X, Yuan C-X *et al.*, 2002. The earliest known eutherian mammal. *Nature*, 416(6883): 816–822.

Ji Q, Luo Z X, Zhang X L *et al.*, 2009. Evolutionary development of the middle ear in Mesozoic therian mammals. *Science*, 326(5950): 278–281.

Li C K, Wang Y Q, Hu Y M *et al*., 2003. A new species of *Gobiconodon* (Triconodonta, Mammalia) and its implication for the age of Jehol Biota. *Chinese Sci Bull*, 48(11): 1129–1134.

Luo Z X, Chen P J, Li G *et al*., 2007. A new eutriconodont mammal and evolutionary development in early mammals. *Nature*, 446(7133): 288–293.

Luo Z X, Ji Q, Wible J R *et al.*, 2003. An Early Cretaceous tribosphenic mammal and metatherian evolution. *Science*, 302(5652): 1934–1940.

Luo Z X, Ji Q, Yuan C X, 2007. Convergent dental adaptations in pseudo-tribosphenic and tribosphenic mammals. *Nature*, 450: 93–97.

Meng J, Hu Y M, Wang Y Q *et al.*, 2003. The ossified Meckel's cartilage and internal groove in Mesozoic mammaliaforms: implications to origin of the definitive mammalian middle ear. *Zool J Linn* Soc, 138(4): 431–448.

Meng J, Hu Y M, Wang Y Q *et al*., 2006. A Mesozoic gliding mammal from northeastern China. *Nature*, 444(7121): 889–893.

Ni X J, Hu Y M, Wang Y Q *et al.*, 2005. A clue to the Asian origin of euprimates. *Anthrop Sci,* 113: 3–9.

Ni X J, Meng J, Beard K C *et al.*, 2010. A new tarkadectine primate from the Eocene of Inner Mongolia, China: phylogenetic and biogeographic implications. *Proc R Soc B: Biol Sci*, 277(1679): 247–256.

Ni X J, Wang Y Q, Hu Y M *et al.*, 2004. A euprimate skull from the early Eocene of China. *Nature*, 427(6969): 65–68.

Wang Y, Clemens W A, Hu Y *et al.*, 1998. A probable pseudo-tribosphenic upper molar from the Late Jurassic of China and the early radiation of the holotheria. *J Vert Paleont*, 18(4): 777–787.

Wang Y Q, Hu Y M, Meng J *et al*., 2001. An ossified Meckel's Cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science*, 294(5541): 357–361.

Wang Y Q, Meng J, Beard K C *et al.*, 2010 (in press). Early Paleogene mammalian biochronology of Erlian Basin, Nei Mongol and its relations to climate change. *Sci Sin Terr*.

Wang Y Q, Meng J, Ni X J *et al*., 2007. Major events of Paleogene mammal radiation in China. *Geol J*, 42: 415–430.

Wang Y Q, Tong Y S, Li Q, 2010 (in press). The Chinese continental Paleocene-Eocene boundary and its correlation. *Acta Geol Sin*.